ON THE DEVELOPMENT OF THE

LEAF AND SPOROCARP

IN MARSILIA QUADRIFOLIA, L.

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Dissertation presented to the Board of University Studies of the Johns Hopkins University for the degree of Doctor of Philosophy,

by

Duncan S. Johnson.

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The Leaf and Sporocarp of Marsilia.

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Both genera of the Marsiliaceae have been the subject of frequent study by botanists since the early part of this century. But in spite of this the exact origin, sequence and development of the various organs of the mature sporophyte, and especially the morphological significance of the sporocarp, have never been made out satisfactorily in either genus. This is undoubtedly due *in the main* to the dense covering of trichomes, over all the young organs, which practically prevents the successful study of these parts in toto as transparent objects. But it is due partly also to the complexity of the apical bud with its confusion of numerous and crowded, root, branch, leaf and sporocarp rudiments, developing, except the last, in rapid succession from the segments of the apical cell of the stem. Still much has been accomplished even with this method and with hand sections, by Bischoff, Mettenius, Hanstein and Russow. The introduction of the paraffine method of sectioning has largely overcome the first difficulty, while making the second perhaps more puzzling still. This method in the hands of Meunier, Büsgen, Campbell and others, has added considerably to our knowledge of the minuter details of development in these forms.

The present work was undertaken at the suggestion of

Dr. J. P. Lotsy, then of the Johns Hopkins University, for the purpose of determining the origin and early development of the sporocarp in Marsilia, in the hope that thus some light might be thrown on the question of its morphological nature. It was very soon decided, that the best way to reach this end would be to study in detail the origin and development of the leaf also, for comparison, and thus if possible to complete the detailed developmental history between the leaf mother cell and the sporangium.

The work has been carried on during the last two winters in the biological laboratory of the Johns Hopkins University, under the direction of Dr. J. E. Humphrey, to whom for his constant assistance and encouraging interest, I wish here to express my sincere thanks. I am indebted also to Dr. W. A. Setchell, then of Yale University, for aid in obtaining material.

The material used was obtained from New Haven, Conn. and Cromwell, Conn. It was fixed in either 95% alcohol, 1% chromic acid, or a sublimate-acetic mixture (5% of glacial acetic acid in a saturated solution of corrosive sublimate). All of these gave good results, but the sublimate mixture was the best on the whole, since the chromic acid specimens did not always stain well and at certain stages of development the alcohol caused shrinkage. The material was stained either <u>in toto</u> in Mayer's haemalum, or on the slide with this alone or in combination with Bismarck brown, with gentian

violet or alcoholic cochineal. Of these the haemalum and haemalum with Bismark brown gave the best results.

The Development of the Leaf.

Practically all that we know of the development of the leaf in Marsilia, is due to the work of J. Hanstein, on the leaves of the young embryo, and it will be necessary to refer to this often as we proceed.

The leaves of Marsilia arise in two rows, one on each of the dorso-lateral surfaces of the stem. Each leaf arises from one of the cells derived from a dorso-lateral segment of the tetrahedral apical cell of the stem. The leaf mother cell is first recognizable when the segment in which it arises, is about the third or fourth in it's series from the apical cell. It is soon distinguished by its larger size, usually by a larger nucleus and by it s bulging beyond the general surface of the stem apex, (L. Figs. 1. 2.).

The first division of the leaf mother cell, is usually by a curved longitudinal anticline, appearing toward the dorsal edge of the cell and with it's concavity facing laterally, (S. W. Fig. 2). The second wall is also a longitudinal anticline near the lateral edge of the mother cell and with its concavity facing dorsally, (S. W. Fig. 1). These walls are also inclined to each other, (Fig. 2.) and there is thus left between them the typical two sided apical cell

of the leaf, shaped like the half of a double convex lens, and with its edges directed respectively toward the base and apex of the stem.

Hanstein ('65) has already shown that the leaf of Marsilia has a two sided apical cell, and he figures it (pl.XIII 16. 17) as having approximately the position given above, but he did not describe the origin of the apical cell except in the leaves of the very young embryo. This agrees in origin shape and position with the apical cell of the leaf as found in most of the other Leptosporangiate Ferns that have been studied. They have been thus described by Hofmeister ('62) in Aspidium, by Strasburger ('73) and Campbell ('93) in Azolla, by Kny ('75) in Ceratopteris, by Klein ('87) in Polypodium, by Bower ('89) in Trichomanes, and by Campbell ('87) in Onoclea. In Pteris however, while the origin and shape of the apical cell are the same, its position, as shown by Hofmeister ('62) and Klein ('84) is exactly at right angles to that found in the other genera mentioned. That is the edges are directed transversely to the stem and segments are cut off toward and away from the stem apex alternately.

In Pilularia, the only other genus of the Marsiliaceae, Bower ('89) and Meunier ('87) describe the apical cell of the leaf as two sided, while Campbell ('93[1] pl 12. '95 pl 13) states that it is tetrahedral, and differs thus from that of

Marsilia. The study of the young seedlings of Pilularia globulifera shows that in both shape and position it agrees entirely with Marsilia and thus with the other forms mentioned above except Pteris.

The two sided apical cell thus formed in Marsilia, continues its growth and activity, cutting off segments alternately towards the dorsal and lateral sides of the stem (Fig. 38), or, since the ventral side of the young leaf looks towards the apex of the stem (Fig. 3), the segments are cut off alternately toward the right and left of the leaf itself. This goes on until about fifteen or sixteen segments have been formed on each side, when the apical cell ceases to function as such and apical growth ends. The exact fate of the apical cell was not made out in the leaf, but it is probable that a periclinal wall is finally formed instead of the usual segment wall, as such a wall was seen several times in the apical cell of the sporocarp. Sadebeck ('73), Kny ('75) and Bower ('84) have actually observed such a wall in the apical cell of the leaf, but they were not able to make out just how many segments were cut off before it appeared.

In Marsilia the great regularity of the divisions in the segments of the leaf, as well as the fact that certain cells remain of the full length of the segment (Fig. 5), make it possible to determine quite exactly the number of segments cut off (Fig. 4). The only doubt is in regard to

the first segments, which fuse with the tissue of the stem, so that it is not certain that the segment numbered 1 in Fig. 4, may not really be the second one. Aside from this the several leaves examined in which apical growth had ended agreed very closely as to the number of segments formed.

The young leaf at the end of segmentation of its apical cell, is about 1mm. long and .15mm. in diameter at the base, and nearly up to this time it has the form of a slightly tapering cone, capped by the bulging apical cell, which curves upward and ventrally (Fig. 4) over the stem apex, by more rapid growth on the lower and dorsal sides. The cross section of the leaf at this stage is almost exactly circular. The leaf not being, until the formation of the *pinnae*, at all flattened or spatulate, as described by Campbell ('95) and figured by Hanstein ('65) in M. Drummondii.

Just before the last few segments are formed, the tenth and eleventh, or eleventh and twelfth, segments from the base on each side, begin to swell out laterally and ventrally to form the first pair of *pinnae* of the lamina (p^1, Fig. 31). Soon after the last segment is cut off from the apical cell, the segments beyond the first pair of *pinnae* develope the second and terminal pair of leaflets (p^2, Fig. 32). If the leaf bears one or more sporocarps, the first of these arises on the lower and anterior side of the petiole from the second segment on its side from the base (Fig. 33). The second

sporocarp if present, or else arise from a segment of the petiole above the second, but usually arises on the first sporocarp near its base, and on the side turned toward the petiole.

The segments of the apical cell of the leaf, or primary marginal cells of Hanstein ('65) and Sadebeck ('74), are quite regular in shape, being curved slices, slightly thicker at the middle of the outer border (Fig. 6) and with a slightly curved inner border where the segments overlap (Fig. 8). The first division wall to appear in these marginal cells is a longitudinal and radial anticline (Fig. 9), running from about the middle of the inner border to the dorsal part of the outer border, so as to cut off about a third of the whole semicircular segment toward the dorsal side (I, Figs. 7 - 10). We may call the third thus cut off a <u>section</u>, and the part still left of the primary marginal cell is the secondary marginal cell (m.c.^{2}, Fig. 9). Wall I is apparently the "tangential wall" of Sadebeck ('74), and <u>section</u> I is the "schichtzelle" of Hanstein ('65). But this terminology does not seem appropriate here, when the real position of this and the later section walls is taken into account, since it refers to the position of the walls at the surface of the leaf only, when the thing of real importance is their position in the interior, as we shall see.

The second wall formed in the segment is also a longi-

tudinal anticline (II Figs. 6, 10), but instead of being radial it is nearly paralell to the inner or median border of the segment, running from wall I to the ventral outer border of the secondary marginal cell, thus cutting off section II and leaving a tertiary marginal cell ($m.c.^3$, Figs. 10. 11). In each of these sections and in the tertiary marginal cell walls are formed in various planes nearly simultaneously as the leaf grows. In section I there is formed first a pericline (pl. w., Fig. 11), at about one third of the distance outward from the center of the leaf, cutting off thus at the inner end a part of the plerome contributed by this section to the axial bundle of the leaf. Then a longitudinal and radial anticline, which we may call the halving anticline, cuts the outer cell into two (h.a., Figs. 7. 11). Meantime the plerome of section II is cut off by a pericline (Fig. 11), while the tertiary marginal cell devides by a transverse anticline ($t.a.^1$, Figs. 6. 7) into an acroscopic and a basiscopic marginal cell. This anticline is the "radial wall" of Sadebeck.

The further divisions can best be described by taking up first the fate of the two tertiary marginal cells. In each of these there is formed first an anticline (III, Fig. 11) nearly paralell to wall I and toward the dorsal side of the marginal cell; then a similar wall is formed toward the ventral side paralell to wall II (IV Figs. 6. 11). There

are thus left two marginal cells of the fifth grade in each segment. The next wall formed in each of these may have either one of two positions. In the more frequent type of division, another longitudinal anticline appears in each (V, Fig. 13) paralell to wall III, forming thus the fifth and last section and leaving an ultimate marginal cell of the sixth grade. Then a pericline appears, running from wall IV to wall V , and the function of the marginal cell as such is thus ended. In the other and less frequent type of division, the marginal cells of the fifth grade are divided immediately by periclines running from wall III to wall IV , the marginal cell of the fifth grade playing the same role here as that of the sixth grade in the first type; and their further development is also practically the same in both cases. The fate of all the segments of the leaf is in other respects the same, with the exception of those giving rise to the lamina and to the sporocarp, in which the pericline is never formed in the marginal cell.

The Petiole.

Taking the first type of leaf for the study of the further development of the segments of the petiole, we find that during the divisions of the tertiary marginal cells, sections I and II, and the other sections as fast as formed,

go on dividing actively. Section I cuts off a dermatogen layer by a pericline near the outer end of each half, then a second plerome portion is cut off from the inner end of each (d. and pl., Fig. 13) and section II, followed by each of the others in turn, cuts off plerome and dermatogen (Figs. 13 - 15), while the ultimate marginal cell is last of all to form, first the dermatogen wall as described above, and then still later the plerome wall (pl. w., Fig. 16). The dermatogen soon splits by a pericline into two layers around the whole circumference of the petiole, and these break up by anticlines, both longitudinal and transverse, to form the epidermis and hypodermis, each of which remains of one cell in thickness even in the mature leaf (ep. hy. Figs. 14 - 19). On the line of the median wall, of each of the section walls, and of the halving anticline of section I, small intercellular spaces soon appear between the cells of the periblem and those of the hypodermis (a.c., Figs. 13 - 19). These are the beginnings of the longitudinal air canals of the petiole, of which, as can be seen from their origin, fourteen are formed altogether in leaves where the segments divide according to this type.

The single periblem cell formed in each half of section I, in each of the other sections and in the ultimate marginal cell (pl. Figs. 13 - 15), soon divides by a pericline into two cells (Fig. 15). Of these the inner cell di-

sides by anticlines and periclines to form the mesophyll cells of the mature leaf (mr., Figs. 15 - 19), while the outer cell gives rise to both the longitudinal and the transverse partitions between the air canals (a.c., Figs. 15, 16). These latter cells swell out in the middle (Figs. 16 - 18) and grow out at the ends into papilla like tips, which are in contact with those of their fellows of the adjacent sections (Figs. 17, 21), leaving an intercellular space between these and the mesophyll cells and also one above and below each papilla, connecting this with the primary air canal formed between the partition cells and the hypodermis (Figs. 16, 17, 21). These papillae are soon cut off by longitudinal anticlines (Figs. 17, 21 - 23), and thus is formed a pair of small nearly isodiametric cells, in each canal opposite each of the primary partition cells, of which there are usually eight in the length of a segment. From these eight pairs of cells, one cell in each pair being from each of the opposite primary partition cells bordering on an air canal, are developed the eight transverse partitions of the air canal in each segment. These remain one cell thick even till maturity, but later in their development many intercellular openings or pores are formed, allowing the passage of air through them. (p. t., Figs. 19, 20, 21). Except for these pores, the partitions of the mature leaf stretch completely across from mem-

papil to hypodermis and from one longitudinal partition to the next.

That part of each primary partition cell left after the separation of the single cross partition cell at each end, does not divide further by longitudinal anticlines, till very much later, but immediately gives rise to the longitudinal partition between the adjacent air canals. As these cells grow in a radial direction they are divided by periclines until, in the mature leaf, the partitions may be fifteen cells or more in radial breadth and form one third the diameter of the petiole, but they are only one cell thick (L.p., Fig. 19, 20). These cells grow with the longitudinal growth of the leaf (Figs. 21 - 24). As each cell elongates it is seen that the primary cross partition cell at one end (c.p.c., Fig. 24) is nearer the acroscopic wall of the longitudinal partition cell, and at the other end is nearer the basiscopic wall. Then when the transverse anticline appears it is somewhat oblique, and thus forms two wedge shaped cells, each with a cross partition cell at the broad end and none at the narrow one (Fig. 25). The cross partitions in adjacent air canals are thus not opposite but alternate. These wedge shaped cells continue to grow and divide frequently by transverse anticlines, till in the mature petiole the cross partitions are far apart. Here in the longitudinal partitions also the

find at maturity many small intercellular openings or pores, the "nóeuds" of Meunier, which allow communication between adjacent canals (L.p.p., Figs. 19, 20, [illegible]).

In the type of petiole with five sections in each segment, there are, as we have seen, fourteen primary air canals. When the segments of both sides of the petiole form only four section walls, there are but twelve canals, while when, as occasionally happens, one side forms four and the other five sections, we find thirteen canals. All three types are found in the older petioles, but it is interesting to note that the only figure of a cross section of a petiole that I have seen, that of Bischoff ('28), is a petiole of the less frequent type with thirteen canals.

At a comparatively late stage of the development of the leaf, when the longi-tudinal partition is already many cells broad radially, the outer cells, next to the hypodermis, or the inner ones next to the mesophyll cells, may split by a longitudinal anticline. The daughter cells then separate laterally (a.c., Fig. I[illegible]), and divide by periclines, forming thus a new canal bordered by these cells and the hypodermis or these and the mesophyll cells. This splitting of the primary partition may apparently proceed through its whole radial width, and thus form a secondary canal be-tween the two layers, hardly to be distinguished from the primary canals in the mature leaf. The number of the sec-

ondary canals thus formed is always small, less than half of the primary ones, but there is apparently no regularity either in number or position.

When the epidermal layer of a section has divided by one longitudinal anticline and three transverse ones (Fig. 27), forming thus eight cells altogether, four in the length of a segment and two in the width of a section, there is cut from each of these cells, by a circular anticline at the acroscopic end, a small cell which gives rise to one of the numerous trichomes that clothe the young leaf. The rest of the original epidermal cell then divides to four cells with the trichome at the acroscopic end of one of the upper pair (Fig. 28), then further divisions follow and at maturity the epidermal cells become much elongated (Fig. 29), as has been shown by Russow ('72) and also by Meunier for Pilularia, while some of them may later form more secondary trichomes. Each trichome cell grows out beyond the surface of the epidermis (Fig. 26) and swells at its outer end to a knob, which soon elongates, in the direction of the length of the petiole. On the basiscopic side it projects but slightly, while it grows out toward the tip of the leaf into the long multicellular hair, which is supported by the basal or stalk cell that remains wedged in between the other epidermal cells (Fig. 30). Before the leaf reaches maturity these hairs separate

from their basal cells and thus leave the leaf [illegible]. The later development and mature structure of these trichomes have been studied by Russow, and have been worked out in great detail by Meunier for the similar ones of Pilularia.

Stomata also occur on the petiole, but apparently not till quite a late stage and their development was not studied.

By the time that the longitudinal partitions are three or four cells in radial width, a longitudinal row of the large mesophyll cells opposite each partition, usually in the next to the inner layer of these, becomes specialized to form one of the so-called tannin sacs (t.s., Figs. 1[illegible], 1[illegible]). The contents of these are distinguished by a brownish color in the unstained alcoholic material, but usually stain very darkly with haemalum. In the mature leaf their cells are about the same size as the surrounding mesophyll cells. The latter are about twice as long as broad and fit together quite squarely at the ends, while laterally they are rounded off from each other, leaving between them many small intercellular spaces (Fig. 20) which connect with the large air canals.

While these structures have been developing from the dermatogen and periblem layers of the petiole, the plerome portions of the first four sections have given rise to the axial vascular bundle. The first plerome cell cut off from

section I together with the two cells [illegible] from the primary periblem of this section, divide rapidly by many periclines and longitudinal anticlines (Figs. [illegible], 13 - 1[illegible]). Later transverse anticlines appear, the first one being in about the tenth segment from the apical cell of a leaf of the size shown in Fig. [illegible]. In section II a longitudinal anticline is formed in the plerome cell paralell to the median wall; then a similar wall perpendicular to this divides the plerome into quarters (Figs. 1[illegible] - 1[illegible]). Of these, the cell in the angle between sections I and III (tr., Figs. [illegible], 1[illegible] - 19) never divides further, but becomes directly the large trachea of its side of the axial bundle. Though no division walls are formed in this its nucleus divides actively, so that in a trachea of half a millimeter in length (Fig. 5), there may be twenty-five or thirty nucleipresent. Later these and the other protoplasmic contents of the trachea disappear, while the end walls, which are portions of the original segment walls, assume gradually the oblique position characteristic of these in the mature trachea (Fig. 5). Their inclination is always downwards and dorsal as shown in the figure. This is the only cell of the segment that remains of the full length of a segment for any considerable time during the development.

The other three quarters of this section, and all the

plerome of sections III and IV divide up like the plerome of section I, by frequent periclines and longitudinal anticlines, and by fewer transverse anticlines, to form with this the remaining tissues of the axial bundle. The small cells of the outer layer of the bundle gradually become more regular in shape and uniform in size, forming thus the characteristic bundle sheath (b.s., Figs. 18, 19).

The plerome of the ultimate marginalcell never takes any part in the formation of the axial bundle, but in some cases that of section V apparently contributes to the formation of the sheath and of a few cells within this (Fig. 18).

The Lamina.

By the time that the apical cell of the leaf has ceased to cut off segments, the tenth and eleventh (or eleventh and twelfth) segments from the base on each side, have begun to grow out laterally and ventrally to form the first pair of pinnae (p¹, Fig. 31). These pinnae do not correspond in extent exactly with the segment, as they have been shown to do in Asplenium serpentini by Sadebeck ('73) and in Onoclea struthiopteris by Campbell ('87). In this respect they agree rather with the pinnae of Ceratopteris thalictroides, as described by Kny ('75). The lower border

of a pinna (Fig. ??) may correspond exactly with a segment wall while the upper border falls short of the second segment wall above, or perhaps the reverse may be true though it was never seen satisfactorily. It is certain, however, that the lower pinna on each side is formed from the whole length of one leaf segment and the larger part of another, and never of a single segment or of more than two. After cutting off its last segment the apical cell of the leaf, as stated above, probably breaks up to form marginal cells like those formed in the segments. By the time that this has happened, the segments beyond the first pair of pinnae, except all or part of the one next to the pinna on each side, have begun to swell out (Fig. 3?) to form the terminal pair of pinnae. Later on the marginal cells arising from the apical cell probably take part also in the development of these pinnae.

The beginning of the development of a pinna is best seen in a transverse section of the leaf through the pinna, and is practically the same for both pairs. While in the segments of the petiole there are only five section walls formed, and the marginal cell of the sixth grade is the ultimate one, in the segments giving rise to the lamina no periclinal (dermatogen and plerome) walls are ever formed in the marginal cells. These on the contrary continue to form walls parallell to the lower section walls

ill lat in the developmen of the lamina (Figs. ,).
The next wall formed after wall V is toward the ventral side of the marginal cell (VI , Figs. 34, 35), continuing thus the regular alternation of the section walls. Then wall VII is formed toward the dorsal side of the cell, wall VIII toward the ventral side, and so on till a large number of sections, if we may still call them such, have been formed (Fig. 35), the marginal cell being still distinguishable, and probably active, when the pinnae are more than two millimeters broad. These additional sections divide like the earlier ones by periclines to form the plerome, periblem and dermatogen layers and later by anticlines (Fig. 35), forming thus the various tissues of the lamina. Meanwhile the marginal cells divide also by anticlines perpendicular to the edge of the pinna (Fig. 38). They thus constantly increase in number and form a rounded growing edge, as Hanstein ('65) has shown, the pinna finally becoming wedge shaped with a broad rounded outer end, in the mature leaf. The pinnae are directed more ventrally than laterally from the petiole even at the beginning, and those of the upper or younger pair soon come to have their ventral surfaces nearly in contact, while the lower and older pair are folded together in the leaf bud so as to enclose the younger ones between them (Fig.).

A branch of the axial bundle of the petiole is given off to each pinna, and each of these, branches in the pinna to form the anastomosing veins characteristic of the leaves of Marsilia. The detailed development of the bundles of the pinna was not studied, and it is not certain whether they originate as Sadebeck ('74) has shown them to do in Asplenium. The epidermal cells of the leaf give rise to stomata on the upper side, or on both upper and under sides, and to deciduous trichomes like those of the petiole.

In the leaf of Pilularia which was examined for comparison with Marsilia, the segments of the two sided apical cell form out three sections, and leave thus an ultimate marginal cell of the fourth grade. The sections correspond in relative position to the first three in Marsilia, but they and the ultimate marginal cell are broader than in the latter, since the whole semicircular segment is here made up of the four divisions, instead of containing six divisions as in Marsilia. Here as in Marsilia the outer part of section I is split by a pericline into two cells, each of which plays the same role as one of the other whole sections, in the development of the periblem and dermatogen structures. The marginal cell, as well as all of the sections, here takes part in forming the axial bundle, and as will be seen from the number of sections, there

There are only ten primary air canals formed in the leaf, as is figured by Bischoff ('[illegible], VIII, 1[illegible]) and Campbell ('[illegible], XV, 10). The partitions like the sections from which they arise are thicker, and seem to be much more irregular in both size and position, than in Marsilia. The trachea formed in section II of each segment is here less prominent from its size than in the petiole of Marsilia.

The Sporocarp.

The bean shaped sporocarps of Marsilia quadrifolia are most often borne in pairs, the stalks of the two apparently uniting below to form a common stalk, which joins the petiole of the fertile leaf on its inner side near the base. Occasionally only one sporocarp is found on a leaf, or there may be two with their stalks inserted separately on the petiole, and these may be several millimeters apart at maturity. Again, more rarely still, there may be three or four sporocarps, all with a common stalk, or one may arise separately from the petiole while the others are joined to it by a common stalk. In the younger shoots, when the sporocarps are not yet half grown, it is usually found that the smaller or younger one of a pair or of three, is borne on the side of the stalk toward the

petiole from which it arises.

It is usually found that where any sporocarps occur on a branch of the stem, they are present on practically all the leaves of this branch. This fact was of very great assistance in the study of sections of the buds, or slightly developed branches, since the absence of sporocarp rudiments on the older leaves of a bud enabled one then to avoid a fruitless search for the less easily recognizable earliest rudiments, on the younger leaves of the same bud.

It is an interesting fact that of the several localities from which material was obtained, the plants from those habitats where the water level lowered considerably toward the end of the growing season, leaving the plants to grow on the wet mud and in the air, matured many more sporocarps than those which were submerged throughout the entire growing season. This appears not to be due to the fact that fewer sporocarps arise on the leaves of the submerged plants, but rather to the fact that the rudiments which are formed do not complete their development. At the end of July many young sporocarps are found on plants from either habitat, while at the end of September plants that have been left out of the water, by the fall of the water level, have many maturing sporocarps on them and those that are still submerged have very few. Closer examination of the leaves of the sub-

[illegible] plants, however, [illegible] half-grown sporocarps of normal appearance, and many more of the same or smaller size which have evidently been arrested in their development, and appear shrunken or withered. The leaves on which these are borne have gone on in their development, and we may thus find on full grown leaves sporocarps of the same size as those found on other leaves of which the pinnae have not yet unfolded. There is thus, on the whole, no great regularity in the retardation in development of the fertile or sporocarp bearing leaves.

Of the origin of the sporocarp of Marsilia, Bischoff ('28) says, that it arises as a slight prominence or papilla on the anterior side of the base of the petiole. Mettenius ('4) on the other hand, states that it arises endogenously and later breaks through the epidermis of the petiole, to form a projecting solid mass of tissue in the interior of which the various internal structures of the capsule are formed. The youngest sporocarps found by Russo ('72), had a two sided apical cell, but were already differentiated intoasterile stalk and a fertile tip or capsule, being probably in about the same stage as that shown in Fig. 42. He traced the development of the soral canals, stating that they arise by the splitting apart of certain cells in the interior of the capsule, and the development of pits on the ventral surface of the

into which the spaces finally open, leaving the soral canals thus open to the exterior for a time, to be closed again later by the growing together of the cells at the ventral surface. On the outer walls of these cavities arise the "soral cells", in each of which walls appear later so as to cut out a tetrahedral apical cell. This cuts off a number of segments, which according to Russow give rise to the placenta with its vascular bundle, and to the microsporangia, then a pericline appears at the inner end of the apical cell forming thus the archesporium of the single macrosporangium arising from it. Goebel ('82) states that the soral canals of Marsilia are external in origin and that the sporangia arise from superficial cells. Büsgen ('90) described the earliest stage of the sporocarp as in one case a "gap" (Lücke) in the epidermal tissue of the young leaf near its base, and in another place as a swelling or prominence in the same region. The sporocarp grows for a time by a two sided apical cell, and he thinks it probable that all of the soral cells are derived from an epidermal cell of the ventral side of the capsule. The placenta macrosporangia and microsporangia he states are all formed as Russow has shown from these soral cells.

In the similar sporocarp of Pilularia, Hofmeister ('62) and Juranyi ('79) describe the soral cavities as arising internally, while Goebel ('82), Meunier ('87) and

Campbell ('[illegible]) [illegible] origin as Goebel and Büsgen had found to be the case in Marsilia.

According to my own observations on Marsilia quadrifolia, the sporocarp first makes its appearance when the young leaf on which it is borne, consists of about six or seven segments on each side; thus long before the lamina, or even the segments that are to develope this, have been formed. It arises by the increase in size and bulging out, of apparently either, the acroscopic or the basiscopic ultimate marginal cell, of what is probably the second segment on its side from the base of the leaf (Fig. 37). Because of the beginning of curvature of the leaf, the proximity of the sporocarp rudiment to the axillary bud of the same leaf and the resulting difficulty in orienting so as to get exactly longitudinal sections of the leaf through the sporocarp rudiment, it was impossible to decide certainly in which segment the latter arises. It is probably the second rather than either the first or third segment, and cannot be a younger one than the latter in any of the cases seen, and though no indication of this was seen, it is possible that the exact point of origin may be shown, on further observation to vary. The sporocarp always arises from a marginal cell of the inner and ventral side of the young petiole (Fig. 3[illegible]), the tip of which at this time is beginning to take a position nearl

parallel to the stem (Fig. [illegible]1). Soon there appears in the sporocarp mother cell, a curved anticline nearly parallel to either its acroscopic or its basiscopic wall, then a similar transverse anticline on the opposite side of the mother cell (Figs. 3[illegible], 39), and there is thus formed a two sided apical cell like that of the leaf, with its edges directed across the leaf. The sporocarp, as it arises thus from the whole of a marginal cell, which has not yet given rise to the three meristem layers that it is capable of forming, is not, strictly speaking, epidermal in origin. In its origin, by a two sided apical cell formed in a marginal cell of the leaf, the sporocarp resembles closely the solitary sporangium of Lygodium, which as was shown by Prantl (Sadebeck '82, Fig. 64) arises from a marginal cell of the fertile pinnule.

The apical cell of the sporocarp thus formed goes on cutting off segments alternately toward and away from the leaf apex, which are to form the right and left sides of the sporocarp, till more than twenty have been formed on each side. It thus gives rise to a slightly tapering conical structure, much like the young leaf, which bends laterally to grow up beside the leaf (Fig. [illegible]1) with its ventral side facing in the same direction, but soon begins to bend ventrally upon itself (Fig. 4[illegible]). Finally about the time that apical growth ceases, the upper part or cap-

sule lies with its ventral side nearly in contact with that of the lower or stalk portion of the sporocarp (Fig. 43). There is never any curling in of the extreme tip of the sporocarp suggesting the circinate coiling of the leaf, and the bending mentioned is later partially straightened out, as Russow ('72) has shown by the more rapid growth of the ventral side of the capsule. The activity of the apical cell as such, is ended by the appearance in it of a wall, which in a horizontal section is apparently a periclinal, but its exact direction was not made out satisfactorily in sagittal sections. At the time when this wall appears the bending mentioned above has taken place, the capsule is a millimeter long,, and the sori at the base of this are developed as far as that shown in Fig. 70.

The first few pairs of segments of the sporocarp, probably four or five, form the sterile stalk, and the rest develope the fertile tip or capsule. Of the segments of the capsule the first three pairs do not develope sori and only the youngest one forms a lateral bundle. Each segment of the next eight or nine pairs gives rise to a single sorus and to a lateral branch of the dorsal bundle of the capsule. Beyond the last of the soral segments are six or seven pairs, of which only the three or four oldest form lateral bundles and none form sori. The capsule

soon b[illegible]co[illegible] [illegible] (F[illegible]. [illegible]), [illegible] its early development is closely appressed [illegible] the petiole (Fig. [illegible]) and thickly covered by the trichomes arising from the capsule itself and from the stalk of the sporocarp. These trichomes have been omitted in all drawings because if they had been drawn they would have hidden the more important details in many of the figures.

The shape and size of the segments cut off from the apical cell here, are very nearly like those of the leaf, and their early divisions are exactly the same. Section walls I and II (Fig. 14) are formed in the same position as in the segments of th e leaf, then the transvers anticline appears in the marginal cell (t.a.[1], Fig. [illegible]) forming two of these o[illegible] the third grade, and section wall III is formed in each of these in the usual position (III , Fig. [illegible]). Thus up to this stage the series of figures given for the leaf (Figs. 7 - 11), is equally suitable for the sporocarp. After the formation of wall III , however, the regular alternation, that continues in the leaf till the last section wall is formed, is here broken by the appearance of wall IV on the dorsal side of the marginal cell and parallel to III , instead of on the ventral side as in the leaf (IV , Fig. [illegible]). Wall V in the sporocarp is then formed toward the ventral side of the marginal cell, in the position o[illegible] [illegible]ll

IV of the leaf segments (V, Fig. [illegible]), and soon after this the last section wall (VI, Fig. [illegible]) is formed near the dorsal side of the marginal cell. The ultimate marginal cell is thus of the seventh grade here, and not of the sixth grade as in the leaf.

When a second sporocarp is formed on a leaf, it usually arises from a marginal cell of the second, or third segment of the first sporocarp on the side of the latter that is turned toward the petiole which bears it (F.2, Fig. 10), and a third sporocarp may probably arise from the second in the same way. The exact origin of the apical cell here in the marginal cell was not seen but it is reasonable to expect it to be like that of the first sporocarp in the marginal cell of the leaf, and the earliest stages seen also indicate that this is true. This origin of the younger sporocarps from the older ones, explains the occurrence of the mature sporocarps in pairs or trios on a common stalk, that was mentioned above. But the portion of the stalk of a pair that is common to both is not, as suggested by A. Braun ('70), formed by the fusion of two originally separate stalks, but it is the lower portion of the simple stalk of the older sporocarp, and so of the common stalk of the second and third sporocarps of a trio.

Where two sporocarps are inserted on the petiole or seg-

arate stage, it is probable that they will arise from marginal cells of the petiole, but this is a comparatively rare occurrence and was not actually seen in an early stage of development.

We may return now to the further development of the segments of the sporocarp. The positions of section walls as given above is in general that found in all the segments, but there are frequent exceptions to this in various segments that are worthy of note. Thus section V is unusually broder in the acroscopic marginal cell of the soral segments than in the basiscopic cell (V, Figs. 49, 50). Sometimes section IV is also slightly broader and thus since section VI does not vary greatly in size, the basiscopic ultimate marginal cells, which are evidently the "sorus mother cells" of Büsgen, are the largest ones of the whole sporocarp. It quite frequently happens also that wall IV when formed, in the acroscopic marginal cells of the soral segments and in either marginal cell of the other segments, may bend down at the inner end and intersect wall III instead of running through to meet wall II as usual (IV, Fig. 48). This was frequently seen in the younger stages as figured and in later stages in the segments of the stalk but was never seen in the basiscopic marginal cell of the soral segments. Again, any marginal cell of the sporocarp except the basiscopic one of

[illegible] cells [illegible]
[illegible] V [illegible]
of the sixth grade [illegible] one. This is apparently
analogous to the behavior of some marginal cells of the
fifth grade in the leaf.

The Stalk.

If we follow out the development of each of the six sections or the different regions of the sporocarp, we may best begin with the four or five pairs of segments of the stalk. We shall find that these together produce at maturity a structure much like the peticle of of the leaf, of about half a millimeter in diameter and from ten to twenty millimeters in length. Each of the sections of these segments cuts off plerome and dermatogen cells, and section I cuts off a second portion of plerome as in the leaf, but only the plerome of sections I and III, and usually only part of section III (Fig. 0), take part in forming the axial bundle of the stalk. The plerome of the other sections, together with the periblem of all the sections, developes into the thick walled mesophyll cells, if we may call them such, which give the mature stalk its rigidity and strength, and some of which [illegible]

[illegible] lower [illegible] base of the [illegible] capsule (l.l., Fig. [illegible]). The dermatogen gives rise as in the petiole to the hypodermis, and to the epidermis with its trichomes and stomata, while between the hypodermis and the periblem are formed the small and irregular air canals. There are often more than twenty of these, and six on each side arise between the periblem and hypodermis of sections I and III. It is worthy of note that the dermatogen of sections II and V soon splits by longitudinal anticlines (Fig. 70) as was seen in the leaf (Figs. 15, 1[illegible]), and differs from the dermatogen of the same sections in the soral segments of the capsule, as we shall see later. None of the mesophyll cells either here or elsewhere in the sporocarp become specialized as tannin reservoirs as we have seen them do in the leaf.

The Capsule.

Turning now to the development of the seventeen or eighteen segments of the capsule, we find that each section forms plerome and dermatogen as in the stalk, with the periblem between (pl., pb., d., Figs. [illegible] – [illegible], 71), and that only the two plerome portions of section I take part in forming the dorsal bundle of the capsule [illegible]

sheath ([illegible], Fig. [illegible]). Some of the cells of the plerome portion of section I [illegible] the full length of the segment, but no other cells of the capsule were found to do this. The longitudinal vascular bundle of the sporocarp is thus very much more localized than that of the leaf, which has been seen to arise from the plerome of four of the sections. The dermatogen of all the sections in all the segments of the capsule splits as in the leaf into epidermal and hypodermal layers. Of these the former remains, as in the leaf, of one cell in thickness and gives rise to trichomes and stomata. The latter, as has been shown by Russow and in Pilularia by Meunier, devides (hy., Figs. [illegible], [illegible]) to form the two layers of thickened cells of the wall of the mature capsule, and differs thus from the one layered hypodermis of the petiole (Fig. [illegible]). In general the periblem of all the sections, in all the segments, gives rise to the few layers of loosely packed cells between the vascular bundle and the hypodermis. Between these cells and the hypodermis are formed the small and irregular air canals, which in the capsule are confined largely to the dorsal side and thus to sections I and III (a.c., Fig. [illegible]).

It will be best now to examine in detail first the further development of the eight or nine soral segments, then of the three basal segments and finally of [illegible].

[illegible] ventral segments [illegible] capsule.
We have seen above that section I in the soral segments, as well as in the other segments of this part of the sporocarp, developes much as in the segments of the stalk or of the petiole except for the peculiar specialization of the hypodermis. All the other sections on the contrary have a peculiar history differing from those of either the stalk or the leaf. Sections III , IV and V , dorsal to the marginal cell, widen rapidly at their outer ends, and, as sections II and V do not widen in this way, the ultimate marginal cell is pushed into a ventral position (Figs. [illegible], [illegible], 51). Of course the interpolation of the extra section IV , dorsal to the marginal cell, would give the latter a more ventral position than it has in the petiole (Figs. 1[illegible], 1[illegible]), and this is evident because of its formation out of the normal sequence, but this result is greatly enhanced by its very vigorous expansion at the outer end. Finally section VI grows out at the ventral end, beyond the cells arising from the basiscopic marginal cell and spreads over into contact with the cells of section V at the ventral surface (Figs. [illegible], [illegible]). The plerome of the basiscopic or soral half of section III breaks up by one anticline and then by periclines (Figs. 51, 55) to form the dorsal part of the lateral bundle. The more dorsal part of section IV does likewise, while

in the more ventral part, as we shall see later, the [illegible] forms of the lateral bundle arise in the acroscopic or [illegible] halves of the segments (l.b.f. Fig. [illegible]). In section VI the pleroma of the basiscopic half gives rise to the placental bundle of the sorus and to the branch connecting this with the lateral bundle (pa.b., pa.br., Figs. [illegible] - [illegible], [illegible]).

Of the sections on the ventral side of the marginal cell, the pleroma of section II divides to form rather large isodiametric cells (pl.^{II} Figs. 51, 54) which ultimately form the gelatinizing tissue of the dorsal part of the capsule described by Hanstein ('[illegible]) and Russow ('[illegible]). The pleroma of section V divides by a longitudinal and radial anticline (l.a., Figs. 47, 51) and grows around under the inner end of the cells of the sorus, and the inner end of section VI (Figs. 51 - 54). The ultimate fate of the pleroma of this section is probably to help form the dorsal part of the gelatinous ring along with that of section II. It may also help to form the stalk by which the indusium is connected to this ring, but the development of this was not followed out in detail in the later stages and therefore no definite statement can be made. The periblem of both these sections developes very slightly as far as followed, and as that of section V is pushed around under the base of the sorus (Fig. [illegible]) it

apparently also take part in the formation of the whole of the indusium. The meristogen of both these sections grows very rapidly in a radial direction, keeping pace with the lengthening of the sorus, and giving rise thus to a part of the indusium surrounding the latter (Figs. 51 - 54), becoming finally more than half the width of the capsule (i.ind.,o.ind., Fig. 55). The outer end of these layers later spread out peripherally to meet the ventral end of section VI and thus enclose the cells of the sorus. This portion of each of these two sections becomes several cells in thickness (Figs. 54, 55), and gives rise to a part at least of the ventral portion of the gelatinous ring, while the inner portions (o.ind.,i.ind., Fig. 54) remain one cell thick even till maturity. This latter statement, however, is strictly true only of the basicopic portions of these segments, as we shall see later.

The Sporangia.

It remains to describe the development of the most important division of the soral segments, the basicopic ultimate marginal cell. This has a very interesting and significant history, since each is the mother cell of all the sporangia of the sorus formed in its segment. It is the "sorus mother cell" of Büsgen, [illegible]

[illegible] but to a part of the indusium as well, this name is not strictly appropriate. There is, as we shall see, no single cell after the two tertiary marginal cells are formed which gives rise to the placenta and sporangia only, nor to these and the whole of the indusium. No true dermatogen wall is ever formed in this marginal cell, hence the placenta and sporangia are not of strictly epidermal origin. They are formed rather, as was found in the origin of the sporocarp from the leaf, from a cell that is capable of forming at least two meristem layers, as it actually does in the segments of the stalk (Fig. 50).

In the growth of this part of the capsule that takes place soon after section VI is formed, the marginal cell elongates in a radial direction. At the same time its wall begins to separate at the outer or ventral end from the outer cells of section V (s.c., Fig. 51). Meanwhile the marginal cell has grown in the direction of the length of the sporocarp also (Figs. 5[illegible], 64). It soon splits by a transverse anticline into halves, of which the acroscopic one soon comes to be the larger. Then each of these divides by another transverse anticline (Fig. [illegible]) forming thus four cells, of which the basicopic cell of the two formed in the acroscopic cell of the first pair soon becomes the largest (p.m. - sp.m.c., Fig. [illegible]), and since [illegible]

cell giving rise to the mother cell of all the macro-sporangia of the sorus, we may call it the primary macro-sporangium mother cell. The sister cell of this latter divides once more by a transverse anticline (Figs. [illegible], [illegible]) and thus five cells are formed from the basiscopic marginal cell, two on each side of the primary macrosporangium mother cell. Of these the one next to the latter on each side (p.mi - sp.m.c., Figs. 5[illegible], [illegible]4) is a primary microsporangium mother cell, each giving rise to all the microsporangia of the sorus on its side of the placenta. The outer cell on each side (i.ind., Figs. 5[illegible], [illegible]4) forms the inner layer of the lateral part of the indusium. These five cells are at first much alike as they appear in a transverse section of the capsule (Fig. 51), but the contents of the three middle ones soon become much denser (Fig. [illegible]7).

In horizontal section it is soon seen that while the outer or indusial cells, of the five, remain in contact with the cells of section V , the three middle or sporangium mother cells are separated from these by a narrow slit (s.c., Fig. [illegible]7). This is the beginning of the soral canal that we have already noticed in the cross section (s.c., Fig. [illegible]1). This cavity constantly increases in size by the pushing out of the indusial cells on each side of the sorus and the forcing away thus of the cells of section V from the sporangium mother cells.

D[illegible] marginal cell the acroscopic one splits, usually by one transverse anticline (Figs. [illegible]), into two cells, one of which helps to form the outer layer of the [illegible] indusium in its own segment, while the other goes [illegible] for the sorus of the next younger segment (o.ind., Figs. [illegible], [illegible]0).

Returning now to the development of the five cells formed in the basiscopic marginal cell as seen in a cross section of the capsule, we find that at first it is very similar for all, and we may take for further study, sections in the plane of the macrosporangium mother cell. This is seen to elongate radially and then to divide by a periclinе (Fig. 52), then by further growth and division of both of the cells thus formed (ma-sp.m.c., Fig. 5[illegible]) there arises a row of seven or eight cells reaching from about the center of the capsule nearly to the ventral surface (Fig. 5[illegible]), all of which are separated by the soral cavity from the cells of the inner layer of the indusium arising in section V. From the increase in size of both of the cells formed from the marginal cell by the first periclinе, from the occurrence of nuclear spindles in both, and from their relation to the surrounding cells, there can be no doubt that both divide further and give rise to

all of the macrosporangium mother cells of the sorus. None of the latter then can be developed from cells of the capsule dorsal to the marginal cells as Büsgen ('90) thought possible. In sagittal section (Fig. [illegible]) it may be seen that, as suggested above, periclinal walls are formed in the microsporangium mother cells and the inner indusial cells about opposite those in the macrosporangium mother cells, as they keep pace with these in radial growth.

By the time that the whole number of macrosporangium mother cells has been formed in the sorus, the soral canal has bent away from the median wall below and slanted toward the median wall at the ventral end (Fig. [illegible]). It is sometimes the case as Büsgen has pointed out that the sporangial cells may grow over into contact with the inner layer of the indusium, but there is certainly no growing together after the first separation and the phenomenon has no significance. Soon after the soral canal has taken this curved form the cells of sections V and VI come into contact and thus close the outer end of the canal. These soon fuse together firmly but the line of junction remains visible for a long time, (Fig. [illegible]).

While the five divisions of the basiscopic marginal cell have increased in numbers by radial growth they have also been developing in other directions. The soral cavity, or canal is at first considerably [illegible] ventral

[illegible] (s.c., Figs. [illegible], [illegible]), [illegible] the [illegible] by R[illegible] ('[illegible]). The macrosporangium mother cells push out into this cavity (ma - sp.m.c., Figs. [illegible], [illegible]0), far beyond the microspo-rangium mother cells and swell to many times their origi-nal size. For this reason sagittal sections a little nearer or the median wall than that shown in Fig. [illegible]7 would not show anything of the microsporangium mother cells, but simply the soral cavity and the two layers of the [illegible], on each side of the macrosporangium mother cells, and the microsporangium mother cells might thus easily be over-looked.

As the microsporangium cell grows and swells laterally to a wedge like form, with a rounded outer end, it is also pushed out into the soral cavity, by the growth of the plerome cells of the acroscopic part of the basiscopic half of section VI (pl.b., Figs. [illegible], [illegible]0). Meantime the microsporangium mother cell on each side has increased in thickness and divided by an anticline parallel to the segment wall (mi - sp.m.c., Fig. [illegible]0), Then each of the resulting cells divides by a similar wall (Fig. [illegible]1) and thus four cells are formed on each side of the macrospo-rangium mother cell. These are pushed around by the growth of the macrosporangium mother cells to a position nearly at right angles to their original one (Fig. [illegible]2). The [illegible]

[illegible] (') [illegible]

formed from the lower segment of the apical cell of the macrosporangium.

The macrosporangium mother cell divides by walls in three planes which thus form a tetrahedral apical cell between them (ma.sp., Figs. [illegible], 61). The first wall formed as seen in a cross section of the capsule is usually toward the ventral side of the mother cell (Fig. [illegible]). There is no crowding off of the mother cells from each other in the sorus as described by Büsgen ('90) and as figured in Pilularia by Meunier ('87), but these lie squarely against each other (Figs. [illegible], 54). The apical cell of the macrosporangium cuts off two segments on each side which form the lateral and basal walls of the sporangium and that part of the placenta or stalk which lies between the sporangium and the region of the placental bundle (Fig. [illegible]). Then a periclinal is formed near the outer end of the apical cell and the archesporium is thus cut out (arc., Fig. 62) and the sporangium wall completed, the former giving rise as Russow has shown to the tapetum and spores.

While the macrosporangium has been developing thus, there have been important changes in the cells derived from the microsporangium mother cells and in the cells of section VI that are pushing in between these. Each of the four cells [illegible]

divides by walls perpendicular [illegible] usually into four cells at first. Thus are produced four rows, of approximately thirty-two cells each, on either side in the length of a sorus of eight macrosporangia. There would thus be four cells opposite each macrosporangium in a sagittal section of a capsule a little older than that shown in Fig. [illegible]. Each of the cells arising from that one of the original four nearest the microsporangium (mi - sp., Figs. [illegible]1, [illegible]2) swells out from the placenta and divides into a basal cell, and an outer cell which gives rise by inclined walls to the tetrahedral apical cell of a microsporangium; while the cells derived from the original four farthest from the macrosporangium, form the outer cells of the placenta in that region (pa., Figs. [illegible]1, [illegible]2). The basal cell of the microsporangium can perhaps be considered as homologous with the stalk cell found in the sporangia of many of the homosporous Leptosporangiates, but there was nothing seen in the development of the macrosporangium that could be regarded as such, and Marsilia thus differs from Pilularia, in which Campbell ('[illegible]) has described such a cell as being sometimes formed.

The cells derived from the plerome of section VI as described above, continue their growth, giving rise to two rows of cells, as seen in horizontal section (Figs.

0 - [illegible]), [illegible] placental [illegible] cells on each side derived from the [illegible] cells. From certain of these [illegible] cells, in a way to be described in detail later, are formed the placental bundle and the placental branch.

Meanwhile the inner and outer indusial cells, on each side of the sorus, have kept pace with the growth of the sporangial cells. The acroscopic part of section V and the acroscopic marginal cell have each split by a transverse anticline (Fig. [illegible]) to form the lateral part of the outer layer of the indusia of the adjacent sori, and these, in connection with the cells of section II, complete the outer indusial layer, surrounding the sorus through its whole length (o.ind., Figs. [illegible], [illegible]0 - [illegible]). The lateral inner indusial cells, arising from the basiscopic marginal cell, together with the cells of the basiscopic half of section V complete the inner layer of the indusium also. Each of these layers remains of a single layer in thickness even at maturity, as no division walls are formed in their cells except those perpendicular to the surface, and by growth in this manner the indusium constantly increases the size of the sorus cavity as the sporangia are pushing out into them (Figs. [illegible]0 - [illegible]). During the growth of the indusium some intercellular spaces appear, between the two layers, [illegible]

[illegible] adjacent sori, [illegible] (? – l.c., Fig. ?). Finally, [illegible] on either side of these spaces, the [illegible] of each [illegible] become entirely separated from those of the other [illegible] (Fig. ?). By this time also the [illegible] of the capsule push into the furrows between sori on the opposite side (Fig. ?). They then appear to [illegible] on opposite sides of the capsule, and [illegible] above (Fig. ?) they are also alternate in their origin; but [illegible] their origin they may often appear to be [illegible] opposite, as a result of the unequal growth [illegible] the two sides of the capsule.

The primary microsporangium mother cells are thus shown to be sister cells of the primary macrosporangium mother cells, and are differentiated from these before the latter begin to divide [illegible] microsporangium mother cells. Hence they can not arise from segments of the apical cell [illegible] as [illegible] and Büsgen believed. The placental [illegible] has also been shown to come not from the inner [illegible] of the segments of the apical cell of the macrosporangium as Büsgen and Russow [illegible], nor [illegible] to be derived [illegible] from the marginal cell, but to be formed from the [illegible] of section VI.

The Vascular Bundle System.

We may now turn to the position and development of the lateral bundles and their branches which were not described in connection with the development of the sorus, in order to avoid unnecessary complication. The proximal portion of each lateral bundle arises from the basiscopic half of the procambial strands III and IV (l.b., Figs. [illegible] - [illegible], [illegible], [illegible]). At a point near or opposite the inner end of the sorus the lateral bundle splits into three branches as has been shown by Russow. Two of these continue on in the course the single bundle took in the wall of the capsule (l.b.f., Fig. [illegible], [illegible]), while the third turns abruptly inward toward the center and joins the placental bundle (pl.br., Figs. [illegible], [illegible], [illegible]). Of the two outer forks of the lateral bundle, one arises in the basiscopic quarter of the acroscopic half of the same segment (l.b.f., Figs. [illegible], [illegible]), while the other arises from the acroscopic quarter of the acroscopic half of the next older segment (l.b.f., Figs. [illegible], [illegible], [illegible]). These forks are formed while the marginal cell is still undivided, by the periclinal walls that form first in the cells of the sorus (Fig. [illegible]), and grow in length with the sorus (l.b.f., Figs. [illegible], [illegible], [illegible]). They increase also in thickness [illegible]

[illegible] ([illegible], Fig. [illegible] - [illegible]), [illegible] near the [illegible] margin of the segment. [illegible] become connected with those of their fellows of the same side in a more or less regular way by the formation of vascular tissue from the cells lying between them (Fig. [illegible]).

It has been shown above that the plerome of the basi-scopic half of section VII divides into two portions (Fig. [illegible]) and that the acroscopic one of these furnishes the median cells of the placenta (pa., Fig. [illegible]). Most of these cells form a part of the general parenchyma of this region of the placenta, but several rows of these cells at the point between the opposite microsporangia and in contact with the first segment of the apical cell of the macrosporangium, give rise to the placental bundle which runs through the whole length of the placenta. In a region about opposite the inner ends of the sorus (pa. br., Fig. [illegible], [illegible]) these same cells also become specialized to form the placental branch which runs across the whole breadth of section VI from the single portion of the lateral bundle to the placental bundle (pa.br., Figs. [illegible], [illegible], [illegible]).

The sterile Segments of the Capsule.

We come [illegible] to the [illegible] segments of the capsule [illegible]

[illegible] [illegible]. [illegible] showing

at the base of the capsule give rise, [illegible] the sepal segments, to its portion of the dorsal bundle from the plerome of section I. The plerome of [illegible] gives rise also to a forked lateral bundle, formed in the plerome of sections III and IV as in the sepal segments (Figs. [illegible], [illegible]). No trace of the placental branch or placental bundle is seen here, and in the other two segments no lateral bundle is developed. The plerome of sections II, V and VI, in the youngest segment of the three, and probably that of all the sections except section I of the middle segment, is apparently devoted to the formation of the basal portion of the gelatinous ring (g.r., Figs. [illegible], [illegible]). In the oldest or basal segment of the three the plerome and periblem of all the sections become modified to form the basal wall of two layers of thickened cells (b.w., Figs [illegible], [illegible]), like the hypodermal cells of the capsule wall, and stretching across from the dorsal to the ventral wall. In the periblem of section I in the two younger segments, and probably in the first two sepal segments also, there is developed a wall of thickened cells, like those of the hypodermis, enclosing a lens-shaped mass of less thickened cells, the "lens shaped space" of B[illegible] (l.c., Fig. [illegible]). Into a small opening at the [illegible] end of this space projects [illegible]

[illegible] closer [illegible]

([illegible], Fig. [illegible]). [illegible] dorsal cell there is [illegible] opening through the lower [illegible] the last single cell (Fig. [illegible]). By the greater development of the epidermal cells above this space the upper border or papilla of the [illegible] ([illegible], Fig. [illegible]).

Lastly, in the six or seven pairs of segments at the tip of the capsule there is no single dorsal bundle, as this divides into two just beyond where the lateral bundles of the youngest soral segments arise. These two divisions then run nearly parallel near the dorsal wall of the capsule and each gives off three or four branches, which arise like those of the soral segments, from the phloem of sections III and IV (Figs. [illegible]), and are joined, like these also, with their fellows of the same side near the ventral margin. The exact origin of the two parallel divisions of the dorsal bundle was not made out satisfactorily. The phloem of the first three or four segments aside from that forming the [illegible], and all of that of the remaining segments probably takes part in forming this portion of the gelatinous ring.

Summary.

The typical [illegible]

the direction toward the [illegible]. The [illegible] - [illegible] segments of this, [illegible], by five [illegible] [illegible] and [illegible] periclinal [illegible] divisions, into five sections and an ultimate marginal cell of the sixth grade. Each of these divisions forms plerome, periblem and dermatogen layers, and the axial strand of the petiole is formed from the plerome of the first four sections. Air canals appear between the periblem and dermatogen in a definite number, and the partitions between these, which are derived from the periblem, have many intercellular openings through them at maturity. Trichomes are formed from the epidermal cells in a very regular arrangement. Certain rows of the periblem cells become specialized as tannin reservoirs. The pinnae or divisions of the lamina arise as a result of the continued activity of the marginal cells of certain segments, and their limits do not correspond exactly with those of the segments.

The sporocarp arises from a single ultimate marginal cell of the second segment of the leaf, as a lateral branch of the latter, when it consists of only six or seven segments on each side. The second sporocarp usually arises in the same way from one of the basal marginal cells of the first one, and is thus a secondary branch of the leaf. The apical cell is transverse in position, and [illegible] this continues [illegible]

[illegible] till the capsule [illegible].
The semicircular segments of the apical cell are divided by longitudinal anticlines into six sections and an ultimate marginal cell of the seventh plane. The dorsal bundle of the capsule is formed entirely from the plerome of section I, the lateral bundles in part from sections III and IV and the placental bundle and branches in section VI. The epidermis is of one layer of cells and the hypodermis of two, both layers of the latter consisting of very thick walled cells. The trichomes of the epidermis and the air canals under the hypodermis are like those of the petiole, except that the latter are smaller and more irregular. The sporangia of each sorus are all derived from a basiscopic ultimate marginal cell, which gives rise also to the cells forming the inner layer of the lateral portion of the indusium. The single primary macrosporangium mother cell and the two primary microsporangium mother cells of each sorus are sister cells, formed by the first divisions of the marginal cell. They are thus superficial, but not strictly epidermal, in origin. The sorus canal arises by a split between the walls of the primary sporangium mother cells and those of the cells of section V, beginning at the ventral [illegible] of the capsule and extending [illegible] to the inner [illegible] of the former. From the [illegible] so formed is developed the

The stalk cell, as [illegible] in large [illegible] growth and division of the primary sporangium mother cells, which form thus also the ultimate sporangium mother cells. A stalk cell is formed in the development of the microsporangium, but nothing homologous with this was seen in the case of the macrosporangium. The indusium of each sorus arises partly within its own segment, but partly also from the next older segment. It is derived from the dermatogen cells of sections II and V and from the marginal cells. The gelatinizing tissue of the dorsal part of the capsule arises largely, if not entirely, from the plerome of section II ; that of the ventral side from the dermatogen of sections II and V , and that at either end of the capsule probably comes from all three meristem layers.

Conclusions.

The leaf of Marsilia agrees closely with those of most of the leptosporangiate Ferns which have been studied, in its origin, in its growth by a two sided apical cell, and in the development of the lamina by the continued activity of the marginal cells of certain of its segments. The position of the primary or section walls in the segments of the leaf, while agreeing closely with

that found in Asplenium [illegible] by S[illegible] ('), is very different from that figured by Campbell (' p. 32[illegible]) for the Leptosporangiates in general, so far as one can judge from the description alone. It is very evident that, as Bower has suggested, there is great need of detailed work on the origin of the meristem layers in the various organs of the Ferns. Many of the accounts at present available, of the development of the petiole and lamina are very unsatisfactory because of the lack of details in both descriptions and figures.

The sporocarp is certainly to be considered as a branch of the leaf, since it is derived from the apical cell of the leaf. The second sporocarp is usually a branch of the first and hence a secondary branch of the leaf, while the third may in like manner be a tertiary branch. In the shape of its apical cell and of the segments cut off from this, the sporocarp agrees exactly with the leaf, while in the primary divisions of the segments, it differs from the leaf only in the interpolation of an extra section dorsal to the marginal cell. The [illegible], so far as its development gives any clue, is homologous with the petiole only of the leaf. There is no indication from this source that the sporocarp contains anything homologous with the lamina of the leaf. The out-growths of the superficial cells [illegible],

[illegible] to Goebel' [illegible]
sion. We may [illegible]
in morphological [illegible] as well as in physiological func-
tion.

It is difficult however to see how the view of Goebel that the capsule of Marsilia represents a single leaflet folded together with its edges meeting at the ventral margin of the capsule, is to be harmonized with the facts of development as given above. The same difficulty is of course found in the interpretation of Russow and Büsgen who regard the capsule as a pair of leaflets, and in that of Meunier and Campbell who consider it a pinnate leaf with the rachis at the dorsal margin and with a pinna for each sorus.

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Explanation of Figures.

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Abbreviations used :- A. direction of the apex; [illegible], [illegible] of the [illegible]; [illegible].c., [illegible] cell; ar. arch- esporium; a.s.w. acroscopic segment wall; B. direction of base; b.c.tc. basal cell of trichome; b.m.c. basiscopic marginal cell; Br. branch, (axial bud); [illegible] [illegible] cells; b.s. bundle sheath; b.s.w. basiscopic segment wall; b.w. basal wall of capsule; C. capsule; c.[illegible] transverse partition; c.t.c. transverse partition cell; c.[illegible] pores in transverse partition; D. dorsal side; [illegible] [illegible]; ^{I} ^{II} etc. [illegible] of [illegible] I, II etc. ; d.b. dorsal bundle of sporocarp; d.[illegible] [illegible] wall; ep. epidermis; F. sporocarp; F^{1} first sporocarp; F^{2} second sporocarp; F.m.c. mother cell of sporocarp; [illegible] gelatinous ring; h.[illegible] [illegible] of section I ; hy. hypodermis; ind. indusium; i.ind. inner layer of indusium; i.s. intercellular space ; i.s.c. [illegible] cavity; L. leaf; l.[illegible] longitudinal [illegible] in plerome of section V ; l.b. lateral branch of dorsal bundle; l.[illegible] [illegible] of the lateral branch; l.[illegible] longitudinal partition; l.p.c. longitudinal partition cell; l.p.[illegible] pores in longi- tudinal partition; l.[illegible] lower [illegible]; m.[illegible] [illegible];

[illegible] ; [illegible] ;

[illegible]^1, [illegible]^2 --etc. [illegible] cell [illegible] , [illegible] , [illegible], [illegible]; [illegible]; [illegible] macro-sporangium mother cell; [illegible] mesophyll; [illegible] cell; [illegible] outer layer of [illegible] of capsule; [illegible] outer layer of indusium; [illegible]^1 [illegible]; [illegible]^2 [illegible]; [illegible] lacuna; [illegible] placental [illegible]; [illegible] placental branch; pl.^{I} periblem of section I ; pl.^{II} periblem of section II ; p. periblem; p.c. partition cell; pl. plerome ; pl.^{1} first plerome portion of section I ; pl.^{2} second plerome portion of section I ; pl.^{I} plerome of section I ; pl.^{II} plerome of section II ; [illegible] plerome cell; [illegible] primary macrosporangium mother cell; [illegible] primary microsporangium mother cell ; S. [illegible] ; s.c. seed cavity; st. stalk; st.b. stalk bundle; [illegible] [illegible] cell of microsporangium; [illegible] [illegible] cell; [illegible]^1 [illegible]^2 --etc. first, second,--etc. transverse anticlines of marginal cells; [illegible] [illegible]; ta. tapetum; [illegible] [illegible]; [illegible] [illegible]; [illegible] [illegible]; V. ventral side; [illegible] apical cell; I. II. III. --etc. first, second,--etc. section walls; 1. 2. 3.--etc. first, second, --etc. segments of the apical cell on one side.

All figures are camera drawings, [illegible] [illegible] microscope [illegible] [illegible] L., [illegible] Fig. [illegible], [illegible].

Plate I.

Fig. 1. A nearly vertical section of [illegible] stem apex showing the surface of the stem and the leaf mother cell with one segment wall. x300.

Fig. 2. Transverse section of stem [illegible] apical cell of young leaf. x300.

Fig. 3. Section of stem between vertical and hori-zontal planes, showing surface of stem apex and transverse section of leaf. x300.

Fig. 4. Sagittal section of a leaf nearly at the end of apical growth. x200.

Fig. 5. Part of a sagittal section of the petiole of an older leaf. x[illegible]00.

Fig. 6. Ventral surface of tip of an young leaf. x[illegible]00.

Fig. 7. Dorsal surface of the tip of a similar leaf x400.

Fig. [illegible]. Surface of the tip of a very young leaf show-ing the shapes of the two youngest segments on one side and the apical cell [illegible] to show the [illegible] lateral wall and hence the shape of the segment [illegible]. x[illegible]0.

Fig. [illegible]. Half of a nearly transverse section of a young leaf, showing the shape of a segment and the posi-tion of the [illegible] cell [illegible]. x[illegible]0.

Fig. 10. A similar [illegible] [illegible]. x[illegible]0

Fi . 11. A transverse section of ... showing ... segments. x 0

Fi . 12. The ... still older. x 0.

Fig. 13. Transverse section of ... c walls are formed. x 0.

Fi . 14. Transverse section of a petiole showing ... ultimate margin l cell of the fif grade. x 0.

Fig. 15. Similar section showing the ultimate marginal cell of the sixth grade. x 0.

Fig. 16. Transverse section of petiole in which epidermal and hypodermal layers are completed and the ... cells are nearly ready to cut off the ... cells. x 0.

Fig. 17. Part of similar section of a still older petiole. x 00.

Fig. 18. The same section of a still older petiole. x 00.

Fig. 19. Transverse section of a nearly mature petiole. x 0.

Plate II .

Fi . 20. Part of transverse section ... x 00.

Fi . 21. Tangential section of petiole ... x 00.

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Fig. 22. The same in surface view. x 600.

Fig. 23. The same in middle of the petiole. x 600.

Fig. 24. The same still later showing the beginning of the longitudinal partition. x 600.

Fig. 25. Surface view of a longitudinal partition showing the pores in a nearly mature petiole. x 150.

Fig. 26. Sagittal section of petiole, about the region of segment five or six of Fig. 1. x 150.

Fig. 27. Surface view of petiole in the same region showing the arrangement of the trichomes. x 150.

Fig. 28. Later stage of the same. x 150.

Fig. 29. Nearly mature stage of the same. x 600.

Fig. 30. Nearly mature trichome. x 150.

Fig. 31. Horizontal section at the tip of a leaf, showing the beginning of the first pinnae. x 600.

Fig. 32. The same later showing origin of terminal pinnae. x 600.

Fig. 33. Longitudinal section of a leaf through one of the well developed pinnae. x 600.

Fig. 34. Transverse section of leaf through pinnae, a little later than Fig. 31. x 600.

Fig. 35. A similar section still later. x 600.

Fig. 36. A similar section through a leaf [illegible] about two millimeters long. x [illegible].

Fig. 37. A transverse section of petiole [illegible]

[illegible] sporocarp. x[illegible]0.

Fig. [illegible]. Approximately [illegible] section [illegible] showing [illegible] cell [illegible] sporocarp. x[illegible]0.

Fig. [illegible]. The same [illegible]. x[illegible]0.

Fig. [illegible]0. N[illegible] longitudinal section of a stem [illegible] the leaves, an [illegible] and two sporocarp rudiments, showing the under surface of part of side leaf, and cross section of the first sporocarp [illegible], [illegible] of second sporocarp from the first. x [illegible]00.

Plate III.

Fig. [illegible]1. Transverse section of stem, and a young leaf with two sporocarps all nearly parallel to the stem. x1[illegible]0.

Fig. [illegible]. Inner side of young leaf with a sporocarp in which the segmentation of the apical cell is nearly finished. x[illegible].

Fig. [illegible]. An older sporocarp on a petiole showing capsule bent against the stalk. x[illegible].

Fig. [illegible]. Transverse section of a young sporocarp. x[illegible]0.

Fig. [illegible]. The same in an older stage. x[illegible]0.

Fig. [illegible]. Transverse section of capsule [illegible] of the stalk [illegible] formed. x[illegible]0.

Fig. [illegible]. The [illegible] cell, [illegible]. x[illegible]0.

Fig. [illegible]. [illegible] section [illegible] IV [illegible] of [illegible], a little [illegible] Fig. [illegible]. [illegible]0.

Fig. [illegible]. The same [illegible] well [illegible] the relative position of cells IV and V [illegible] marginal cell [illegible]. [illegible]0.

Fig. 50. Transverse section of stalk of [illegible] shown in Fig. 51. x750.

Fig. 51. The same section of capsule [illegible] of beginning of [illegible] canal, showing relative thickness of older and younger walls. [illegible]0.

Fig. [illegible]. Part of transverse section of [illegible] capsule x750.

Fig. 53. The same still older. x400.

Fig. 54. The same at the [illegible] of closing of [illegible] canal. x400.

Fig. [illegible]. The same still later. [illegible].

Fig. [illegible]. Ventral surface of capsule [illegible] Fig. [illegible]. x750.

Plate IV.

Fig. [illegible]. Part of longitudinal section of [illegible] of Fig. [illegible]. [illegible] the ventral surface. [illegible]0.

Fig. [illegible]. The [illegible]. [illegible]0.

Fig. [illegible]. Vertical [illegible] [illegible] sporangium [illegible] 0.

Fig. [illegible]0. Horizontal section of capsule [illegible]

of Fig. [illegible], near [illegible] surface. x[illegible]0.

Fig. [illegible]1. The same, [illegible] as in Fig. [illegible]. x[illegible]0.

Fig. [illegible]. The same [illegible] III [illegible] Fig.

[illegible]. x[illegible]0.

Fig. [illegible]. The same of whole capsule of [illegible]

Fig. [illegible]. x[illegible]0.

Fig. [illegible]. Sagittal section [illegible] cells

of [illegible] b[illegible] same [illegible] as Fig. [illegible]1. x[illegible]0.

Fig. [illegible]. Sagittal section [illegible] III [illegible]

IV of capsule, [illegible] same [illegible]. x[illegible]0.

Fig. [illegible]. The [illegible] of capsule [illegible] Fig.

[illegible]. x[illegible]0.

Fig. [illegible]. Sagittal section [illegible]

x[illegible]0.

Fig. [illegible]. View of inner side of one [illegible] valve [illegible]

a [illegible] of the capsule. x[illegible].

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Vita.

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The writer of this thesis was born in Cromwell, Conn., on the twenty-first day of July 1[illegible]. He received his early education in the public schools of Cromwell and Middletown Conn., and took his college course at Wesleyan University, in the latter town, receiving the degree of B. S. in 1892. During the college year of 1[illegible], he was a graduate student at Wesleyan. Since the fall of 1[illegible] he has been a graduate student at Johns Hopkins University, with Botany as a major subject and Zoology and Physiology as minors.

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